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RELATIONSHIPS OF THE WHITE OAKS OF EASTERN
NORTH AMERICA,

WITH AN INTRODUCTORY SKETCH OF THEIR PHYLOGENETIC HISTORY.¹

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(PLATES IV-VI.)

(Read April 23, 1915.)

I. HISTORY OF THE FAGACEÆ: A RECONSTRUCTION.

Prantl's Classification of the Fagaceæ.

Castaneæ	{ Quercus. Pasania. Castanea.
Fageæ	{ Fagus. Nothofagus.

The five or six genera of the family Fagaceæ to which the oaks belong were well differentiated at least as far back as the Cretaceous age. The beeches are sharply separated from the remainder of the family (the pasanias, chestnuts and oaks), and are undoubtedly the more primitive of the two groups. *Nothofagus*, the genus of primitive beeches, is a characteristically sub-Antarctic genus, still surviving in Tasmania, New Zealand, and the southern part of South America (a South Pacific distribution). *Fagus* itself, once more widely spread, is now found only in Japan, North America and Europe.

The pasanias, chestnuts and oaks are at present in possession of the temperate and tropical regions of Asia, North America, Europe and Mediterranean Africa. Species are most numerous in southeast Asia and in Mexico (regions separated by the Pacific). *Pasania* is limited to southeast Asia, except for one species in California

¹ This paper owes a great deal to the extensive knowledge and the never-failing interest and aid of Dr. William Trelease, under whom the work was done at the University of Illinois in the year 1913-14.

and one in New Zealand (ranges separated by the Pacific). *Castanopsis* (the less specialized chestnuts) is limited to southeast Asia, except for two Californian species (ranges separated by the Pacific). *Castanea* is present in southeast Asia, North America and Europe. *Quercus* has most numerous species in southeast Asia and (especially) Mexico and Central America (regions separated, again, by the Pacific), while the subgenus *Cyclobalanopsis* is limited to southeast Asia (monsoon province). In consideration of the facts that the most primitive genus still lingers on the two sides of the southern Pacific, and that so many other groups are found only in regions bordering on the northern Pacific, it is more than plausible that the family Fagaceæ originated in the Antarctic-Pacific region, and moved northward towards its present northern-hemisphere distribution in the region of the Pacific Ocean. This of course involves the hypothesis of an ancient Cretaceous or pre-Cretaceous Pacific continent—for which there is much other distributional evidence and which Scharff,² among others, holds to be highly probable. The broad similarity of the ranges of *Pasania*, *Castanopsis* and *Cyclobalanopsis* was undoubtedly determined at this early time. The problem of the extension of certain species of *Fagus* and *Castanea* to Europe seems entirely separate, and probably belongs to a more recent period. *Quercus* is involved with both the older and the more modern distribution; they have been mapped out here for convenient reference in the coming discussion of *Quercus*.

II. HISTORY OF QUERCUS, HYPOTHETICALLY RECONSTRUCTED.

Oaks, living or fossil, have been reported from every continent. Living species, however, are unknown in the southern hemisphere, except that they are found south of the equator in the East Indies, and among the mountains of Ecuador (localities separated by the Pacific). Species, as was said, are most numerous in Mexico and Central America and in southeast Asia; the subgroup *Cyclobalanopsis* is limited to southeast Asia. Remembering that *Pasania* and *Castanopsis* are almost limited to the same region, and that the pasania-chestnut-oak group of the Fagaceæ shows here a concentration, and a profusion of species, seen nowhere else in the world,

² Scharff, "Distribution and Origin of Life in North America."

it is natural to suppose that this part of Asia (or more probably, to allow for the outlying species in California, and the oaks in Mexico, a region *east* from southeast Asia) has been the center of distribution, and hence the point of origin of the pasania-chestnut-oak group. And *Quercus* itself, with its black oaks limited to America, its *Cyclobalanopsis* limited to southeast Asia, and its numerous white oak species in both places, undoubtedly differentiated from the pasanias (or their ancestors) in one or other of these regions, or more probably between the two. At any rate, the primitive, little-differentiated *Quercus* must have had a distribution that included both regions, as well as the space between them. We are thus brought again to an hypothetical Pacific continent; for since neither black oak nor *Cyclobalanopsis* exists or gives evidence of having existed in western Asia or Europe, any cretaceous or earlier connection of the two regions in that direction is well-nigh inconceivable. (It is unnecessary to suppose that this Pacific land extended much farther north than the equator).

According to our hypothesis, the disappearance of this Pacific land isolated the two extremes of the range of *Quercus*. The genus had already become differentiated; the Asiatic part of the range received the stock of *Cyclobalanopsis* (found nowhere else) as well as the more typical *Quercus* stock. Certain species of *Quercus*, even today, form a part of the oldest Asiatic flora, which holds its own in isolated regions,—in parts of the Himalayas, for instance. Some of these ancient endemic species are the white oaks *Q. lanata*, *semecarpifolia*, and *dilatata*, of which the last is said by Schottky to stand nearest of all oaks to the *Cyclobalanopsis* group. (American black oaks, however, show certain features in common with *Cyclobalanopsis*—apical ovules, type of style).

The American end of the range received a group of oaks of which (according to evidence from distribution and palaeontology) *Quercus chrysolepis* is probably our nearest representative; these may have been the basis of both the black and the white oaks of America. It is suggestive to find that *Q. semecarpifolia* (representative of the ancient oaks of Asia) bears some resemblance to this early American oak. Some of the European oaks are also of this ancient type; but since one, *Q. Ilex*, occurs in both Asia and Europe,

the inference is that they all reached Europe westward from Asia. Though the older fossil evidences in this continent have all been referred to *Q. chrysolepis* (these date back to the Cretaceous), it seems not improbable that types such as *Q. emoryi* and *Q. hypoleuca* were soon present, and that differentiation early took the lines towards our American *black oaks* and *white oaks*. Since in *Cyclobalanopsis*, and in the pasanias, the abortive ovules are carried upward in growth till in the mature acorn they are typically apical, this may be considered the primitive condition in *Quercus*. *Chrysolepis*, which has them only lateral, is on the way towards having them in the basal, white-oak, position. The black oaks, on the contrary, have preserved the primitive character in this as in other particulars.

(Since the black oaks resemble *Cyclobalanopsis* in some ways, it may be that they differentiated from *Cyclobalanopsis*, in the Pacific region, before reaching America. Or all three may have diverged together from the primitive *Quercus*. Distribution may have been such that *Cyclobalanopsis* went to Asia, *Erythrobalanus* to America, *Lepidobalanus* to both.)

Having thus some conception of a possible Cretaceous history for American oaks, black and white, and of their relationship to the ancient types of Old World oaks, we may now limit ourselves to the white oak group in North America (*Leucobalanus*). For the black oaks, being limited to the western hemisphere and becoming only more sharply differentiated, can give us no further light on white oak relationships. To begin with, we may mark off *Leucobalanus* as follows:

QUERCUS.

Cyclobalanopsis: Abortive ovules apical, styles short, subcapitate, often recurved, cup scales grown into a solid ring, fruit ripening in one year, leaves evergreen, tertiary nerves very fine.

Erythrobalanus: Abortive ovules apical, styles elongated, subcapitate, often recurved, acorn tomentose within, cup scales thin, appressed, fruit ripening in two years, leaves deciduous or evergreen, lobes when present with bristle points.

Styles slender or very short and flattened, not cephalated at apex. *Lepidobalanus*.

Cerris: Abortive ovules basal, styles long, tapering, cup scales often long, bractlike, fruit ripening in two years, leaves more or less dentate.

Leucobalanus: Abortive ovules basal, styles very short, spatulate, acorn not tomentose within, cup scales often thickened at base, fruit ripening in one year, leaves deciduous or evergreen, lobes when present rounded.

The most stable characters in this classification seem to be the position of the abortive ovules, the lining of the acorn shell and the form of the style. Appressions of scales, time for ripening fruit, and time of keeping leaves are all more or less variable among the white oaks.

The earliest home of *Leucobalanus* on this continent, using the term to include the white oaks as they separated themselves from the black oaks in America, seems to have been northern Mexico and the southwestern states. The older type (A. below) still predominates in this region, which has probably long been stable, with a climate similar to the present. It is a region which seems to have been for many species a center of distribution to other parts of the continent. Since the Cretaceous, much differentiation has taken place, the main lines of which may be represented by the following division of North American white oaks:

- A. Leaves persistent, usually evergreen, entire, sinuate or dentate, or, if deeper lobed, with pungent tips.
 - 1. Many species, southwestern U. S. and Mexico.
 - 2. *Virginiana* and varieties—an early offshoot.
- B. Leaves deciduous, lobed or divided, or serrate; lobes rounded, obtuse or acute but not pungent.

The evergreen series, represented, say, by *Q. undulata*, is the more direct continuation of the Cretaceous type, the deciduous the more modern form.

It is barely possible that not all of this differentiation took place on this continent. *Leucobalanus* reached Europe at some time; and the possibility that this took place early (by means of Scharff's Mediterranean land bridge), and that the deciduous oaks originated there, rather than on this continent, must be taken into account. Species of this type occur also in Asia, but there seems to be little doubt that they are sharply separated from the ancient Asiatic species like *semecarpifolia*, and reached Asia in the Tertiary from the eastward. The fact that the range of these species, in the Ter-

tiary, was, at the boreal end, continuous from Asia across America to Europe, gives the possibility of the center of distribution being either in Europe or in America. My data on European oaks are insufficient to decide this point; it seems, however, highly probable that the white oaks with thin, deciduous, lobed leaves originated in or near northern Mexico.

The early members of the group *Leucobalanus*, then, marked by entire, evergreen leaves, gave rise, probably in North America, to a form with thin, deciduous, lobed leaves. This type is now dominant over the greater part of the United States, while the older form holds its own in the southwest and in Mexico, where the climate has probably known no great fluctuations since the Cretaceous, and where it still finds suitable dry and arid habitats. This evergreen type occupies the Mexican highlands, Arizona and New Mexico, extending east into Arkansas, and west into California. *Quercus virginiana* seems also to have been a very early offshoot; with its varieties it forms a well-marked coastal group, ranging from North Carolina south along the shores of the Gulf into Mexico (where it stretches inland up the mountain sides), and appearing also on the California coast.

III. DECIDUOUS WHITE OAKS OF NORTH AMERICA.

The oaks with which we are familiar in this part of the country are of the lobed-leaf type. Geographically, at least, there are three parts to this group,—the eastern, the Rocky Mountain, and the Californian lobed-leaf oaks. It is not clear, however, whether or not these geographical groups can be separated taxonomically. They may be parallel groups, cut off from one another comparatively recently; or, possibly, the Californian group may be more closely related to the deciduous oaks of Europe (type *Q. robur*) than it is to the oaks of the Rocky Mountains and the east. The habit, leaf form and texture, and bud form of the Californian oaks have suggestive resemblances to those of the English oak; and it is perhaps not venturing too much to speculate as to whether these oaks, like certain other forms on our Pacific slope, may not have their closest relatives, not in America at all, but in Europe. There is besides at least one oak in California, *Q. sadleriana*, which appears to find its

nearest relatives in the modern Asiatic oaks, which were mentioned as having probably reached Asia in Tertiary times from the eastward. The *gambelii* group in the Rockies and the Atlantic group are apparently the separated branches of the latest developed white oaks (and the Californian oaks are perhaps a third corresponding group), which before glaciation may have succeeded in covering the greater part of the continent. Glaciation left survivors of this forest, it would seem, in two parts of the land—mountainous regions which projected above the ice—the southern Rockies, and the southern Alleghanies. From the one *Q. gambelii* has spread northward, keeping rather closely to the mountains and differentiating numerous but similar species; while from the other the early species (possibly *lyratiformis* and *minor*) have recovered an enormous stretch of territory, and have produced a correspondingly large number of varied species.

IV. WHITE OAKS OF EASTERN NORTH AMERICA.

The white oaks found east of the Rocky Mountains comprise the following species (see key) :

1. <i>breviloba</i>	2. <i>lyrata</i>
<i>durandii</i>	<i>bicolor</i>
	<i>macrocarpa</i>
3. <i>chapmani</i>	4. <i>michauiii</i>
<i>minor</i>	<i>prinus</i>
<i>margareta</i>	<i>muhlenbergii</i> group.
<i>alba</i>	

These species are all of the deciduous, thin-leaved type of *Leucobalanus*, except that *durandii* and *breviloba*, in ranging from Alabama west and south into northern Mexico, show a series of transitions towards the smaller, more entire, evergreen type of leaf. It might be that a careful study of these forms would show them to be transitional in other features also. Their range seems to indicate an ancient center of distribution in the southwest; this again is in sharp contrast to all the other species, which may be referred to a more recent center in the southeast. In short, there seem to be

several reasons for marking off rather sharply *durandii* and *breviloba* from the remainder of the species present in this area, and for suggesting the possibility that they may be a relic from the time of the differentiation of this deciduous section of *Leucobalanus*.

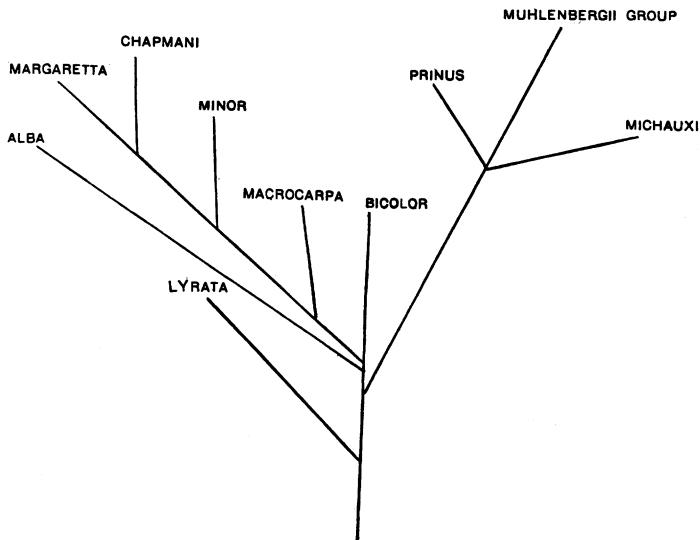
The remainder of the group has a very wide range. It touches the Rockies in Canada, and reaches Texas, Florida, and Maine. Nevertheless, it is almost true to say that every one of the species includes in its range the region of the southern Alleghanies. This region certainly seems to have been a center of distribution after the retreat of the ice fields, for this as well as for certain other groups of plants and animals (*Cambarus*, and the Unionidæ, for instance). The present distribution must have been largely achieved by the Pleistocene, for late Pleistocene fossils indicate a range broadly similar to that of the present.

The species, aside from (1) *durandii* and *breviloba*, fall into three main groups—(2) *macrocarpa* group, (3) *minor* group, (4) *prinus* group. Their relation to one another is not entirely clear. The *macrocarpa* group in some ways holds a central position, which suggests that it may be the oldest. So do the *persistent stipules* of all members of the group; this is without any doubt a primitive character. Its species moreover have the widest range, *macrocarpa* extending in the north to Saskatchewan and Maine, and in a great southward curve with its lowest point well down the Mississippi Valley; south of this it is replaced by *lyrata*. Again, Tertiary leaf-prints which have been referred to deciduous *Quercus* are limited thus far to types resembling *lyrata* and *minor*. (Cockerell's species *lyratiformis* from the Florissant beds is now reported from the John Day Basin, Oregon, where Knowlton also recognizes leaves of the type of *minor*.) There are so many suggestions of this sort that at present we must assume the *macrocarpa* group to be nearest to the ancestral type; and, though the fruit is aberrant, *lyrata* may well stand near the base of the group.

The *minor* group, or at least *minor* itself, has some affinities with *bicolor* and *macrocarpa*. Its wide range and the Tertiary occurrence of this or a similar species show that it has valid claims to antiquity. Whether *alba* belongs in this group is uncertain; it is difficult to see reasons for connecting it closely with any other species. *Mar-*

garettæ, regarded by some as a good species, but which has often been regarded as an *alba-minor* hybrid, suggests such a relationship, but this is more or less doubtful.

The clearest and most highly differentiated group is that of the chestnut oaks. It may be connected with the more typical forms through forms such as *bicolor* (shape of leaf) and *lyrata* (bud-scales). That the serrate leaf is secondarily derived, through a lobed form, and not a persistence of the serration found in older portions of the genus is perhaps not proven; the tendency to lobation rather than serration on young shoots, as well as the general relation of the chestnut oaks to the other oaks of this region make it, however, highly probable.



The above diagram may make more concrete these suggestions concerning relationships.

KEY TO DECIDUOUS WHITE OAKS OF EASTERN NORTH AMERICA.

Leaves deciduous, lobed or dentate, not spinulose.

I. Leaves lobed.

A. Stipules persistent; buds more or less acute.

- 1. Twigs slender, smooth. *Lyrata.*
- 2. Twigs stout, pubescent.
 - a. Fruit sessile, larger; cup usually deeper and fringed. *Macrocarpa.*
 - b. Fruit pedunculate, smaller; cup more shallow, seldom fringed. *Bicolor.*

B. Stipules deciduous; buds rounded.

- 1. Twigs smooth. *Alba.*
- 2. Twigs pubescent.
 - a. Leaves deeply five-lobed, pubescent below. *Minor.*
 - b. Leaves undulate, glabrous below. *Chapmani.*

II. Leaves dentate.

- A. Buds less elongate, leaves narrower, widest near middle. *Muhlenbergii.*
- B. Buds more elongate, leaves broader, widest above middle.
 - 1. Cup scales free at tips only; upper scales very small. *Prinus.*
 - 2. Cup scales free; upper scales often forming a fringe to cup. *Michauxii.*

DESCRIPTION OF PLATES.

PLATE IV. Buds of the rounded type, without stipules. $\times 3$.

FIG. 1. *Q. alba* (Urbana, Illinois).

FIG. 2. *Q. minor* (collected by H. H. Bartlett, Maryland).

PLATE V. Buds of the more acute type, stipules persistent. $\times 3$.

FIG. 1. *Q. macrocarpa* (Urbana, Illinois).

FIG. 2. *Q. bicolor* (Urbana, Illinois).

PLATE VI. Buds of the elongated, chestnut oak type. $\times 3$.

FIG. 1. *Q. prinus* (collected by H. H. Bartlett, Maryland).

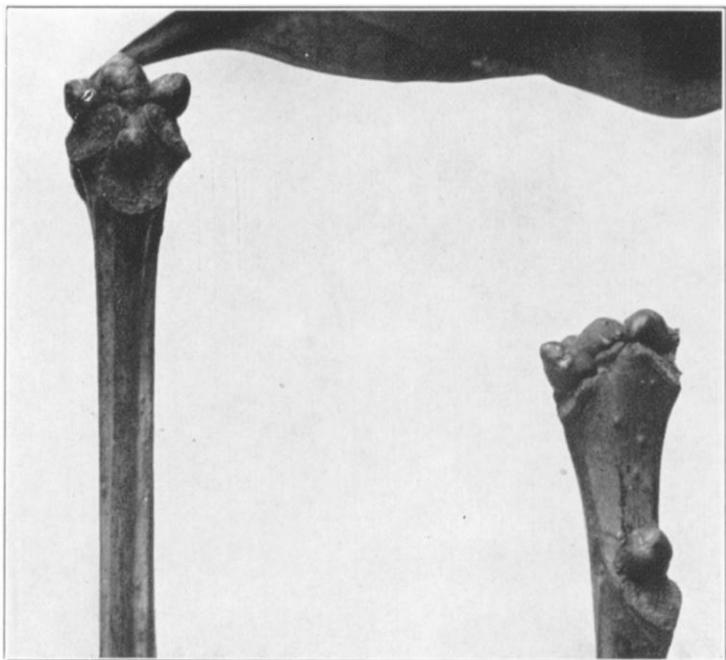


FIG. 1.

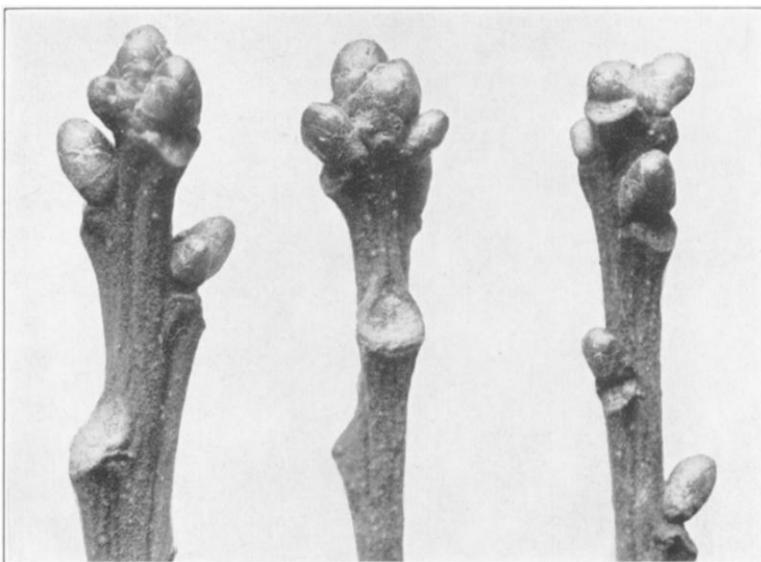


FIG. 2.



FIG. 1.



FIG. 2.



FIG. I.

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